

A new perleidiform (Actinopterygii, Osteichthyes) from the Late Triassic of Northern Italy

Cristina LOMBARDO & Francesca BRAMBILLASCA

C. Lombardo, Dipartimento di Scienze della Terra "A. Desio", Università degli Studi di Milano, Via Mangiagalli 34, I-20133 Milano, Italy; cristina.lombardo@unimi.it

F. Brambillasca, Dipartimento di Scienze della Terra "A. Desio", Università degli Studi di Milano, Via Mangiagalli 34, I-20133 Milano, Italy.

KEY WORDS - *Perleidiformes, Triassic, Adaptive radiation, Durophagy*

ABSTRACT - *Endennia licia* n. gen. n. sp., a new genus of perleidiform from the Zorzino Limestone (Norian, Late Triassic) is here described. The new genus is characterized by a fusiform outline with a strong skull, by fused parietals + dermopterotics and by a peculiar kind of dentition, with long and cylindrical marginal teeth, with flattened apex, and differentiated palatal crushing ones. This kind of dentition, unique among perleidiforms, is indicative that *Endennia licia* n. gen. n. sp. probably fed on organisms with semi-hard or hard exoskeletons, such as small crustaceans or molluscs and echinoderms, which were present also in the Zorzino Limestone. This new taxon adds further data to the knowledge of the perleidiforms, mainly known from Early-Middle Triassic, but recently found to be widespread, also with specialized forms, during the Late Triassic.

RIASSUNTO - [Un nuovo perleidiforme (Osteichthyes, Actinopterygii) dal Triassico Superiore dall'Italia settentrionale] - Viene descritto un nuovo genere e una nuova specie di pesce fossile appartenente ai perleidiformi, *Endennia licia* n. gen. n. sp., proveniente dal Calcere di Zorzino (Norico, Triassico Superiore). Il nuovo genere è caratterizzato da un profilo del corpo fusiforme ed un cranio molto robusto, dalla fusione parziale di alcuni elementi del tetto cranico e da un tipo di dentatura molto particolare, con margini orali di mascella e mandibola dotati di denti lunghi e cilindrici dalla punta leggermente appiattita e denti palatini differenziati e trituranti. Questo tipo di dentatura, unico tra i perleidiformi, porta a ritenere che *Endennia licia* n. gen. n. sp. si nutrisse probabilmente di invertebrati provvisti di esoscheletro sottile quali i crostacei, anche se non si esclude la possibilità che la dieta comprendesse anche piccoli molluschi o echinodermi, la cui presenza è segnalata nella stessa unità stratigrafica, anche sotto forma di frammenti in numerosi coproliti.

Questo nuovo taxon accresce la conoscenza del gruppo dei perleidiformi, molto diffuso nel Triassico Medio, ma che ritrovamenti degli ultimi anni rivelano essere presente, anche con forme molto specializzate, durante il Triassico Superiore.

INTRODUCTION AND GEOLOGICAL SETTING

In the last thirty years the Calcere di Zorzino (Zorzino Limestone, middle Norian, Late Triassic) has yielded an extraordinary rich ichthyofauna: at least 25 genera have been already described or are under study, but probably more than 50 genera are represented (Tintori, 1981, 1983, 1995a, b, 1996a, b; Tintori & Renesto, 1983; Tintori & Sassi, 1992). A few taxa are represented by hundreds or thousands of specimens, like pholidophorids (Zambelli, 1975, 1978, 1980, 1981a, b, 1986), others by dozens and in some cases by few or single specimen. Apart from the numbers, this fauna is important because it records the first major radiation of neopterygians (among these, pycnodonts, semionotids, macrosemiids and pholidophorids), when paleopterygians were still important, especially at the top of the trophic hierarchy, with the "chondrosteans" genera *Birgeria* and *Saurichthys* and the "subholosteans" *Thoracopterus* and *Gubanellia* (Tintori, 1990a; Tintori & Sassi, 1992; Tintori & Lombardo, 1996; Tintori, 1998a).

Reptiles are also very important for the presence of endemic genera and of the oldest pterosaurs so far known. Although the Zorzino Limestone deposited in an intraplatform basin, most reptiles are terrestrial with land (*Langobardisaurus*), arboreal (*Megalancosaurus*)

or flying (*Eudimorphodon*) specializations (Wild, 1978; Renesto, 1994, 2000). These animals probably lived on more or less wide islands situated around the basins; they are usually small-sized, very lightly built, and often have hollow bones: their preservation requires a short post mortem transport in superficial oxic and warm waters. Some others could have spent part of their life in water, especially for feeding, such as the thalattosaur *Endennasaurus*, the armoured placodont *Psephoderma* and the phytosaur *Mystriosuchus* (Renesto, 1992; Renesto & Tintori, 1995; Gozzi & Renesto, 2003).

Invertebrates are also well represented by several crustacean genera (Pinna, 1974; Garassino & Teruzzi, 1993; Basso & Tintori, 1994) echinoderms (echinoids, ophiuroids, crinoids and a single asteroid) (Blake et al., 2000), cnidarians and scleractinia. Gastropods are rare and bivalves are common, mainly as remains of fish predation, and they contributed to constitute the benthic fauna, rich in individuals but poor in species.

The Zorzino Limestone is inferred to have been deposited in a marine basin associated with early Mesozoic rifting (Jadoul et al., 1992, 1994). The basin opened within a wide and thick carbonate platform, the Dolomia Principale Formation, that extended overall of the western margin of the Tethys. Because of the widespread shallow-water environment, connections between the basin and the open sea were probably only

through very long tidal channels, explaining the poorly diversified benthic fauna (Renesto & Tintori, 1995). On the other hand, the restricted environment allowed differentiation of a largely endemic vertebrate fauna including both marine and terrestrial species. Superficially waters were well oxygenated, allowing nekton to thrive, and also at the margins of the basin conditions at bottom were favourable to life. Preservation is usually excellent as almost all the specimens are complete and fully articulated owing to an anoxic bottom and rapid sedimentation (Tintori, 1992). Thin lamination of the fossiliferous levels provides further evidence of an undisturbed bottom at the center of the basin. The fossils found allow reconstruction of life assemblages of both superficial waters and benthic settings at the margins of the basin, as well as those of nearby islands, where terrestrial reptiles could live (Blake et al., 2000).

Abbreviations are as follows: ad, adnasal; ang, angular; ant, antorbital; cl, cleithrum; de, dental; dpt, dermopterotic; exsc, extrascapular; ifo3, infraorbital 3; mx, maxilla; na, nasals; op, operculum; pa, parietal; pcl, postcleithrum; pmx, premaxilla; pop, preoperculum; ppa, postparietal; pt, posttemporal; ro, rostral; sc, scales; scl, supracleithrum; so, supraorbitals; sop, suboperculum.

Institutional abbreviations: MPUM: Museo Paleontologia Università degli Studi di Milano, Milano, Italy; CMISNIO: Civico Museo Insubrico di Storia Naturale, Induno Olona (Varese, Italy).

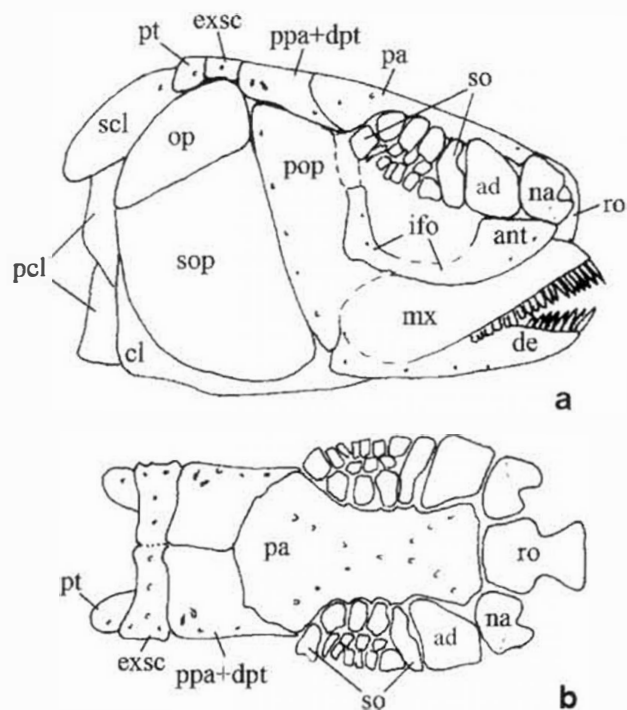


Fig. 1 – *Endennia licia* n. gen. n. sp.: restoration of the skull, a) in lateral and b) in dorsal view.

PALEONTOLOGICAL DESCRIPTION

Order PERLEIDIFORMES Berg, 1937

Family PERLEIDIDAE Brough, 1931

Endennia n. gen.

Diagnosis - As for the only known species.

Type species - *Endennia licia* n. gen. n. sp.

Etymology - From Endenna (Zogno, Bergamo, Lombardy), the name of locality where the holotype has been found.

Type locality - Zogno-Endenna (Bergamo, Italy).

Age - Middle-late Norian (Late Triassic).

Geographical distribution - Bergamo Prealps.

Endennia licia n. gen. n. sp.

Pl. I; Figs. 1-6

Diagnosis (based on a combination of characters) - Medium-sized perleidiform with fusiform body; skull-roof mainly formed by a single expanded parietal plate; total fusion of post-parietal with dermopterotic bones; supraorbital series made of a dozen elements of different size and shape arranged in rows; operculum 1/5 as deep as the suboperculum. Long marginal pencil-like teeth with a flattened cap and big and powerful, partly bicuspidate, crushing teeth disposed in several rows on palatal surface. Squamation consists of 42 scale rows, deeper than broad only in the anterior part of the flanks, ventral and posterior scales broader than deep; posterior margin of the scales slightly serrated, except for the ventral rows. Caudal fin composed of 32 lepidotrichia; 8 epaxial rays.

Etymology - From the Latin word *licia*, which means comb, for the morphology and arrangement of marginal teeth.

Holotype - Specimen MPUM 8434 from Zogno-Endenna site (lower beds). Complete and articulated specimen of 160 mm in total length.

Type locality - Zogno-Endenna (Bergamo, Italy).

Paratypes - Specimen MPUM 8435 (incomplete juvenile specimen) from P8 bed and 8436 (only skull roof) from P10 bed, all Zogno2 site; specimen CMISNIO 267 from Endenna (lower beds), (almost complete and articulated, in 195 mm of total length).

Age and horizon - Uppermost Calcare di Zorzino: middle-late Norian (Late Triassic).

Description - The rostral bone is a very large, subpentagonal element making the snout blunt in outline. The nasal bones are rounded elements irregular in shape; along the anterior margin there is the notch for the anterior narial opening. Each element contacts the

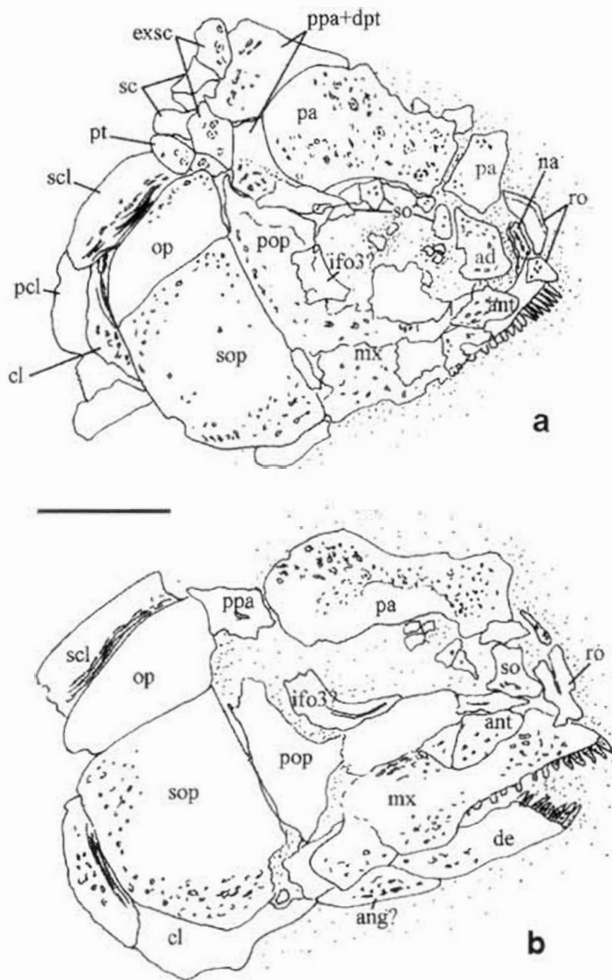


Fig. 2 - *Endennia licia* n. gen. n. sp.: skulls. a) The holotype MPUM 8434. b) Specimen CMISNIO 267. Scale bar = 10 mm.

parietal bone at the anterolateral corner, where the supraorbital sensory canal enters them (Figs. 1-2). The parietal bones are fused medially in a single large plate; it is characterized by large posterior and anterior regions and narrower median one, corresponding to the dorsal margin of the orbit. The posterior outline is strongly convex. The two supraorbital sensory canals run very close to each other medially. The bony plate is ornamented by ganoine ridges and small tubercles, arranged mainly around the pores of the sensory canal (Figs. 1-3). The postparietal and dermopterotic bones of each side are fused to a single, wide L-shaped plate. The anterior, sharply pointed region of this element embraces the postero-lateral margin of the parietal bone, and an anterior and a posterior pit-line are positioned on the postero-ventral corner (Figs. 1-2). The median suture between them is straight and short. The extrascapular bones are sub-trapezoidal; they meet the post-parietals+dermopterotic bones along a straight suture; owing to the state of preservation of the specimens, it is not possible to state if the two extrascapulars were in contact. The supratemporal commissure, typically T-shaped, with patches of

ganoine arranged around each pore, (Figs. 1-2) is well visible. The posttemporal bones are small and rounded elements separated by the elements of the first scale rows (Figs. 1-2). Of the infraorbital series only two fragmented elements have been detected: the trapezoidal large antorbital and the IO3 (?), long and crescentic-shape, abutting the postero-ventral margin of the orbit (Fig. 2). The supraorbital series is very peculiar: it is made of a dozen elements of different size and shape (Figs. 1, 3). The anteriormost element, contacting the nasal bone, is much larger than the others and can be referred to as adnasal in perleidiforms: it has a quadrangular shape and it is followed posteriorly by a mosaic of tesserae seemingly arranged in 3 rows. A clear suture between maxillary and premaxillary bones is not detectable; the powerful maxilla, with an expanded posterior region, bends slightly upwards. The anterior part juts out, being inclined anteroventrally-postero-dorsally; the oral margin is quite straight, hemmed by about twenty teeth. On the anterior part of the maxilla, 7 teeth are relatively longer, pointed and projecting slightly forwards; the others, more backwardly directed, decrease in length and show a different shape, becoming smaller, stouter and blunt (Figs. 1, 2, 4a). The apex of the anteriormost teeth is characterized by a slightly flattened acrodine cup. Teeth different in size and shape are visible on palatal bones, arranged in few (4?) rows: the anteriormost ones are smaller and pointed; medially, teeth are bicuspidate while the posterior ones are very large and completely flattened (Figs. 4b, c). The preopercular bone is backwardly oriented, with straight posterior margin: its outline is not clearly detectable in any specimen, owing to bad preservation of postorbital region, but it seems to be slightly enlarged in the dorsal region; a wide infraorbital process is present. (Figs. 1-2). The operculum is much smaller than the suboperculum, being about 1/5 as deep as the

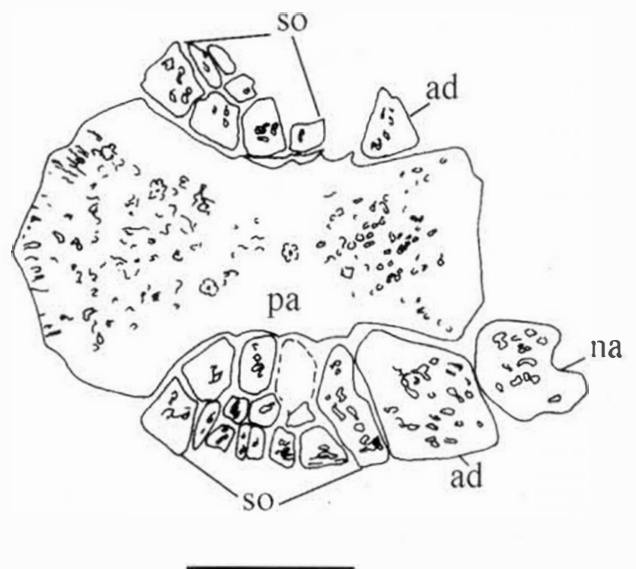


Fig. 3 - *Endennia licia* n. gen. n. sp.: the skull roof as preserved in specimen MPUM 8436. Scale bar = 5 mm.

suboperculum; the dorsal margin is rounded while the suture between operculum and suboperculum is quite straight. The large suboperculum is quadrangular, with a rounded ventral outline. (Figs. 1-2). In specimen CMISNIO 267, the lower jaw is visible in its antero-ventral region: it is a strong element, slightly bend

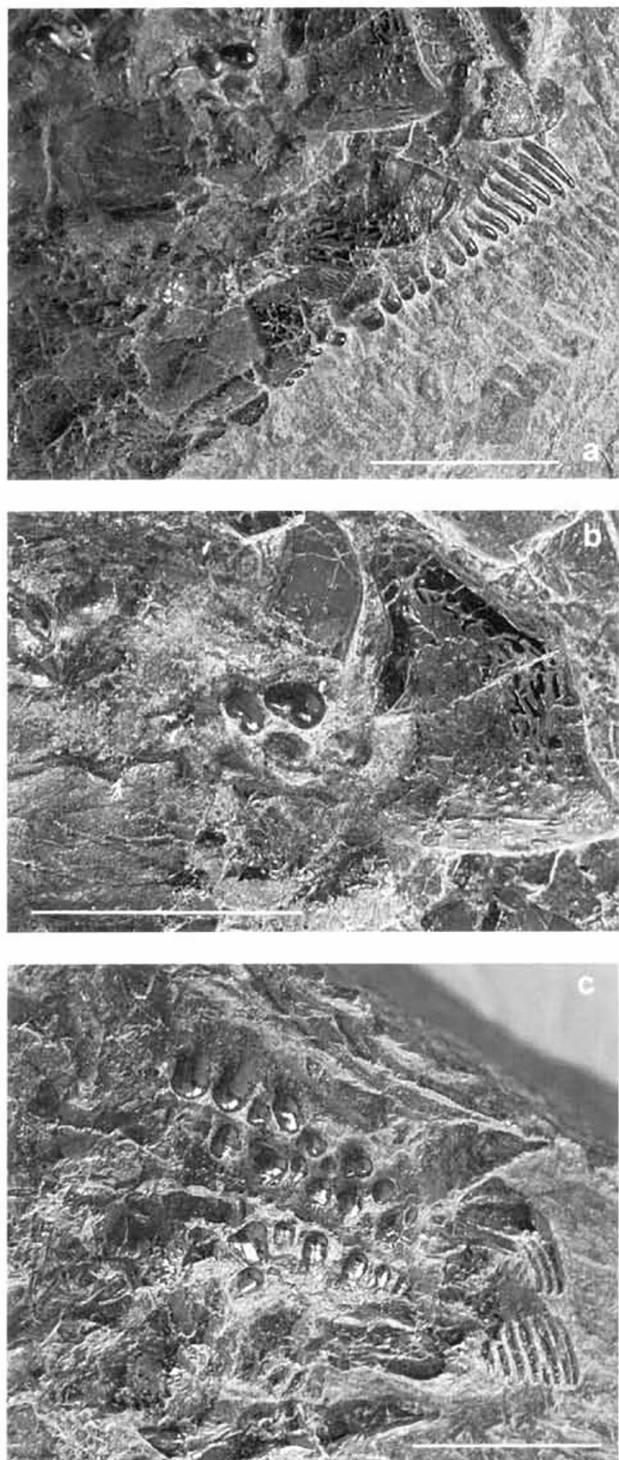


Fig. 4 - *Endemia licia* n. gen. n. sp. a) MPUM 8434: detail of the maxillary dentition. b) Same specimen: palatal teeth; c) MPUM 8435: the skull with palatal and premaxillary dentition. Scale bars = 5 mm.

upwards, bearing at least 6 long and pointed teeth along the anterior oral margin. These teeth are similar in size, shape and arrangement, decreasing in size posteriorly, to the anteriormost ones borne by the maxilla. The dentary is thickly ornamented by tubercles (Fig. 2b). It is not possible to state if branchiostegal rays were present. The cleithrum is crescentic-shaped and ornamented by a series of strong ridges running along its anterior margin. The postcleithrum is subrectangular, deeper than broad, while the supracleithrum is oval-like, showing the same ornamentation of the cleithrum and it is clearly pierced by the sensory canal in its dorsal region: its pores are very conspicuous and surrounded by a ring of tubercles (Fig. 2). The skull bones are ornamented by small ganoine tubercles mainly arranged at the margins of each element.

Fins - The fan-shaped large pectoral fins are composed of at least 15 lepidotrichia: each of them consists of a long proximal segment followed by a series of much shorter, quadrangular distal ones. The first ray carries a series of strong fringing fulcra. At least two spiny basal fulcra have been identified (Pl. 1, fig. 1; Fig. 5a). The pelvic fins are placed at the level of the 17th longitudinal row of scales; each of them consists of at least 9 lepidotrichia, similar in structure to those of the pectorals. The anterior margin of the fins shows a series of fringing fulcra preceded by a couple of basal ones (Pl. 1, fig. 1).

The median fins are relatively small and triangular. The dorsal fin is located at about the level of the 27th row of scales; it is composed of at least 13 lepidotrichia and a series of small fringing fulcra has been observed along the anterior margin. The anal fin, similar in shape to the dorsal one, is composed by at least 9 lepidotrichia (Pl. 1, fig. 1; Fig. 5b) and it is placed at the 27th scales row. In specimen CMISNIO 267 the anal fin is preceded by a couple of modified shield-shaped scale, much larger than the others, identified as the pre-anal scales.

The externally almost symmetrical caudal fin consists of 32 lepidotrichia, with a very short axial body-lobe. There are 8 epaxial rays, with the first two segmented but not branched. Lepidotrichia with the same pattern are present at the base of the ventral lobe of the fin. All the other rays branch at least three times. Strong fringing fulcra and at least two basal fulcra are present on edges of both dorsal and ventral lobe, even if those of the ventral lobe are much smaller (Pl. 1, figs. 1-3; Fig. 6).

Squamation - The squamation consists of 42 transverse scale rows, slightly deeper than broad only on middle-lateral region of the trunk. They decrease in depth both posteriorly and dorso-ventrally: in the dorsal region they become rhombic, as deep as broad. A mid-dorsal row of lanceolate scales is present. Scales of the second horizontal row, below the mid-dorsal ridge, show the openings of the dorsal lateral line. The scales covering the posterior part of the body, those behind the dorsal fin and the caudal peduncle, and in the ventral region of the trunk are broader than deep. The region between the pectoral fins is covered with very small rhombic scales (Pl. 1, figs. 1-3; Figs. 5b,c).

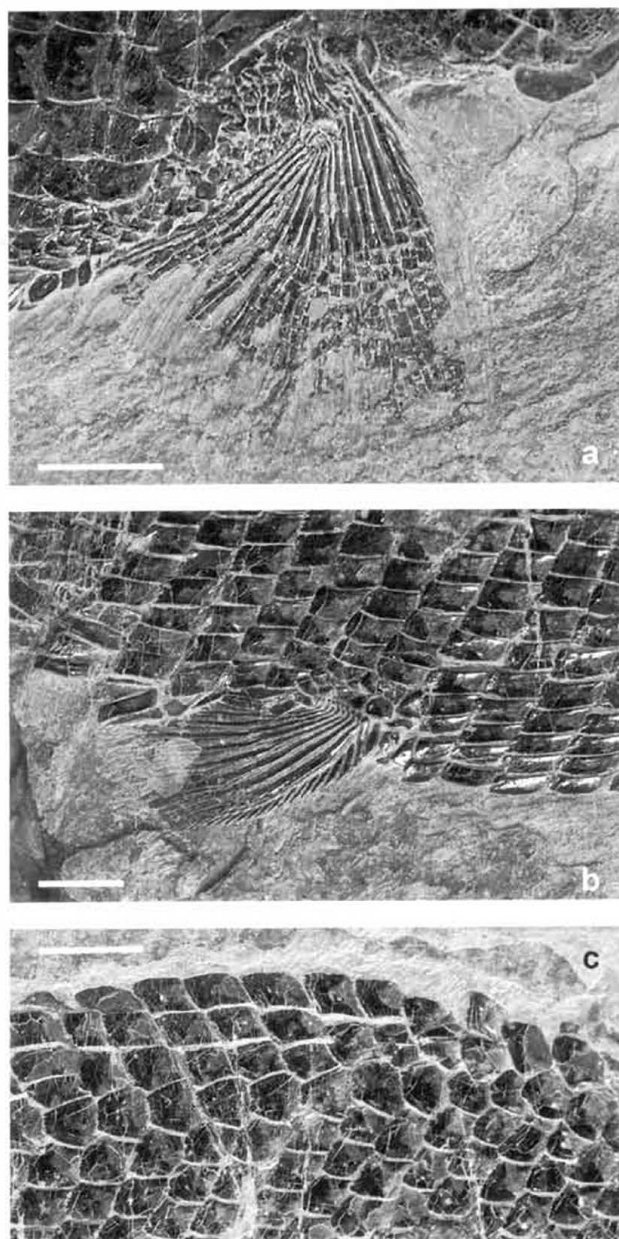


Fig. 5 - *Endennia licia* n. gen. n. sp.: MPUM 8434. a) The right pectoral fin; b) The anal fin and detail of the ventral scales. c) Mid-dorsal scales. Scale bars = 5 mm.

All the scales are thick and smooth and show posterior serration, except for those covering the caudal peduncle and the belly region, where they show a straight posterior margin. The articulation between the scales of the same vertical row seems to have been relatively loose: in specimens MPUM 8434 and CMISNIO 267, which are complete and articulated, scale covering appears “disturbed”, with the scales of most of the longitudinal rows showing little or not at all dorsal and ventral overlapping (Pl. 1, figs. 2-3); this was probably due to a small antero-dorsal articular processes, as visible on MPUM 8434.

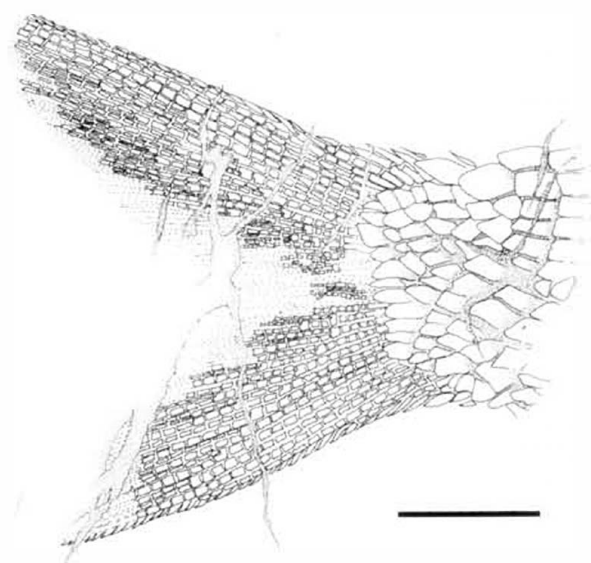


Fig. 6 - *Endennia licia* n. gen. n. sp.: caudal fin of the holotype MPUM 8434. Scale bar = 10 mm.

DISCUSSION

SYSTEMATICS

Endennia licia n. gen. n. sp. belongs to Perleidiformes for the general skull pattern, with a vertically oriented preoperculum, a maxilla with an expanded posterior region, and a medial pentagonal rostral. Also the advanced fins structure is characteristic of perleidiforms, and in general of the so-called “subholosteans” sensu Brough (1939), with an equal ratio between radials and lepidotrichia; these latter have long unsegmented proximal elements and shorter distal ones, as in neopterygians. The body lobe of the tail is very short and the caudal fin is characterized by epaxial rays, inserted dorsally to the notochord. Perleidiformes have been recently considered as a heterogeneous assemblage (Mutter, 2004); nevertheless, at moment we find still preferable to use the “classical” definition of previous authors (among others, see Hutchinson, 1973; Gardiner, 1988; Gardiner & Schaeffer, 1989; Bärgin, 1992; Tintori & Lombardo, 1996; Lombardo & Tintori, 2004), since we believe that the unique combination of dermal skull pattern, structure of the median and caudal fins and the lateral scales deeper than wide on the anterior region of the body, represents an effective tool to identify unequivocally the representatives of this group.

Among Perleidiformes, the characteristics shown by the new genus match those of the family Perleididae (including the genera *Perleidus*, *Meridensia*, *Aetheodontus*, *Ctenognathichthys*, *Peltoperleidus*, *Dipteronotus*, *Daninia*; Bärgin, 1992; Tintori, 1998b; Lombardo, 2001) with the operculum generally smaller than the suboperculum, the preoperculum dorsally expanded and narrower ventrally and the body covered by thick but smooth ganoid scales, scales of the middle-lateral part of the trunk moderately deeper than broad.

Endennia licia n. gen. n. sp. shares with Perleididae also the number of epaxial fin rays (six or seven), the presence of a stout dentition on palatal bones and the post-temporals separated by a couple of scales, even if at least the first two characters are present in most of the perleidiform taxa.

Endennia n. gen. shows a medium-sized fusiform body, covered by thick scales with serrated posterior margin in the posterior flank, slightly deeper than broad on the antero-lateral region of the trunk; all the fins are relatively small. The surface of skull bones is densely ornamented with ganoine ridges and tubercles and the dentition is well developed, both that of the oral margins and the palatal elements. For the body outline, the operculum/suboperculum size ratio and the shape and arrangement of anterior marginal teeth, *Endennia* n. gen. is reminiscent of some species belonging to the perleidid genera *Peltoperleichus* and *Ctenognathichthys*, both from the lower Ladinian of Monte San Giorgio (Bürgin, 1992). With *Peltoperleichus macrodontus* *Endennia* n. gen. shares the pattern of the opercular region, with the operculum much smaller than the suboperculum, and the fusion of part of the skull roof; moreover, *P. macrodontus* shows elongate and protruding marginal teeth, as *Endennia* n. gen. does. Actually, patterns of dentition of the two taxa are dissimilar, being the teeth of *P. macrodontus* not differentiated, only decreasing in size posteriorly; the marginal dentition of *Endennia* n. gen. is on the contrary characterized by teeth of diverse morphologies: long and pointed anteriorly and short and blunt in the posterior region of the jaws. Concerning the fusion of elements of the skull roof, *P. macrodontus* shows fused post-parietals (Bürgin, 1992) but in *Endennia* n. gen. the fusion is between the two frontals, as well as between each parietal + dermopterotic. Also the squamation pattern in *P. macrodontus* is quite different from that of *Endennia* n. gen.: in fact there are less horizontal scale rows and the lateral scales are much deeper than broad.

Concerning *Ctenognathichthys bellottii*, it is very similar to *Endennia* n. gen. in body outline and position of the fins, with the anal and dorsal ones located far behind the middle of the body length (Bürgin, 1992; Tintori, 1998b). Also *Ctenognathichthys* shows a peculiar dentition, made of large, fang-like teeth on the oral margin of both upper and lower jaws and smaller teeth on coronoids elements (Bürgin, 1992, 1996). In spite of this, there are remarkable differences between these two taxa: the marginal teeth of *Endennia* n. gen. are very elongate, but they are not as long as in *Ctenognathichthys bellottii*; besides, *Endennia* n. gen. has large and differentiated crushing teeth on palatal bones, lacking in *Ctenognathichthys*. The shape of preoperculum and consequently the orientation of the opercular region are other features that separate *Endennia* gen. n. from *Ctenognathichthys bellottii*. Both genera show a broad and massive preopercular bone, but in *Endennia* n. gen. it is dorso-ventrally elongate and shows a straight posterior margin, while in *Ctenognathichthys bellottii* it is clearly bent anteriorly. In *Endennia* n. gen. both the upper and lower jaws are much longer and, different from *Ctenognathichthys*

bellottii, the maxilla has teeth also in its middle portion. *Endennia* n. gen. shows a skull roof where the two parietals are fused and an operculum which is about 1/5 of the depth of suboperculum: in *Ctenognathichthys bellottii* parietals are clearly separated and the operculum is only slightly smaller than the suboperculum. Also appearance of the scales is very different: the scales of the anterior part of the flank of *Ctenognathichthys* are ornamented with irregular small concavities and narrow grooves horizontally arranged, while in *Endennia* gen. n. all scales are smooth.

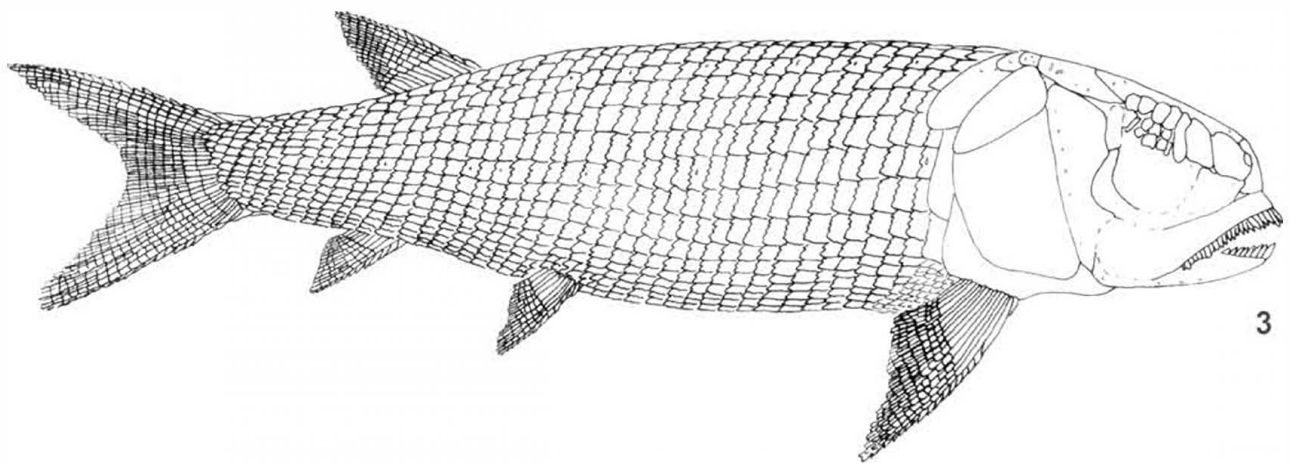
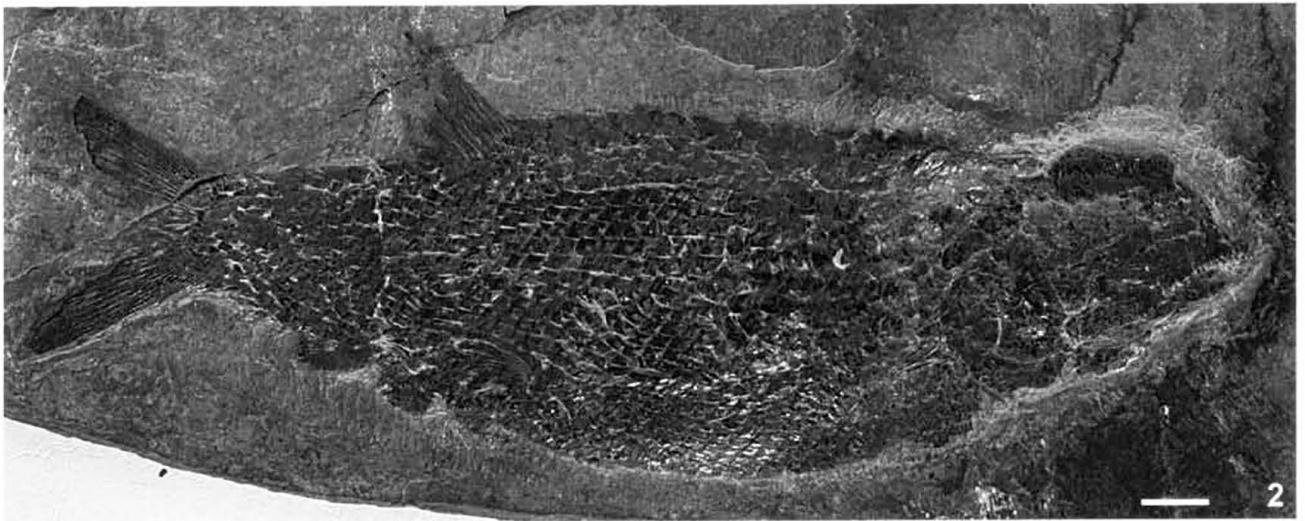
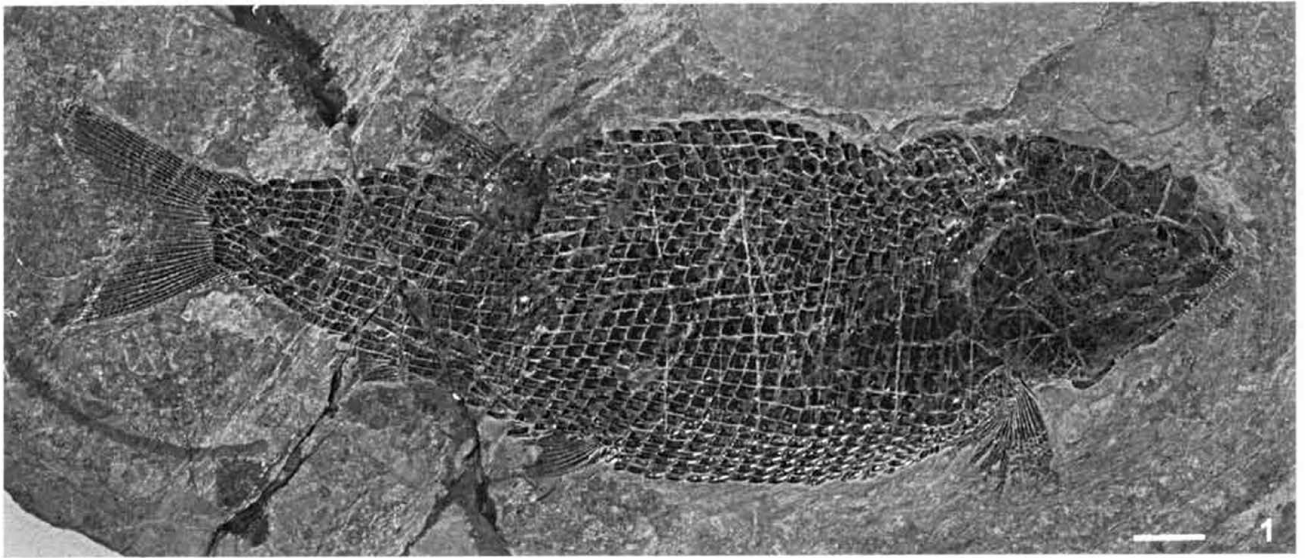
Other perleidids show specialized long marginal teeth: *Felberia excelsa* (Lombardo & Tintori, 2004) and "*Dipteronotus*" *ornatus* (Bürgin, 1992), but these species are clearly different in having a deep bodied habitus and short gapes, provided with marginal teeth only anteriorly. Moreover, their skulls lack the supraorbitals arranged in rows and in the opercular region the operculum is at least as deep as the suboperculum. Marginal teeth are different from the inner ones, but dentition of the same region does not show differentiation, since teeth change only in size.

So *Endennia licia* n. gen. n. sp. shows a combination of characters, such as the rows of supraorbitals and the ventral scales broader than deep, not found in any known taxon of Perleididae. In particular, the new genus shows a peculiar dentition, different from that of the other representatives of the family. In most of them, in fact, adapted to a semi-durophagous diet, teeth borne by the oral margin of both upper and lower jaws are peg-like while palatal ones, irregularly arranged on bony elements, are generally very small, domed and provided with an acrodin cap. Crushing teeth generally show a morphology similar to that of grasping ones, being only larger. There are only few exception: for example, the Early Triassic forms, such as *Cleithrolepis*, *Hydropessum* and *Cleithrolepidina*, show slender toothless, or almost toothless, lower jaw (Hutchinson, 1973); the Ladinian genus *Ctenognathichthys* apparently lacks crushing palatal teeth (Bürgin, 1996), while *Felberia* shows long marginal teeth, with spatulate apex and blunt inner ones (Lombardo & Tintori, 2004). In *Endennia licia* n. gen. n. sp. outer and inner teeth are completely different; besides, there are morphological differences even among teeth borne by the same elements. The anteriormost teeth of maxilla are long and conical, while posteriorly teeth are short and blunt. On the palatal elements, the dentition consists of teeth which are pointed anteriorly, bicuspidate medially and very large and completely flattened posteriorly; moreover, they are arranged in quite regular longitudinal rows.

The possession of an unique combination of characters makes it indispensable to erect the new taxon *Endennia licia* n. gen. n. sp. within the family Perleididae.

FEEDING STRATEGY

Concerning mode of feeding, *Endennia licia* n. gen. n. sp. can be compared with the neopterygians, owing to its fully-durophagous dentition. Even if in the Middle



EXPLANATION OF PLATE 1

- Figs. 1-3 - *Endennia licia* n. gen. n. sp. Scale bars = 10 mm.
1 - The holotype MPUM 8434.
2 - Specimen CMISNIO 267.
3 - Restoration.

Triassic some "subholosteans" have reached a partially tritritural dentition (Bürgin, 1996; Tintori, 1998a), highly specialized durophagous actinopterygians become common and diversified only in the Norian, especially with semionotids and pycnodonts (Tintori, 1998a). In *Sargodon tomicus*, for example, palatal teeth are large and hemispherical and they are arranged in more or less regular rows; pointed teeth are arranged anteriorly and laterally to the hemispherical ones. *Sargodon* also has incisiviform teeth, hamming premaxilla and dentary. For these characteristics, this semionotid is presumed to have fed upon hard-shelled organisms, grasped with the chisel-like teeth and crushed with the grinding inner ones (Tintori, 1983). Pycnodonts are even more specialized in durophagy, both in body shape, which is deep and laterally compressed, and mouth morphology: prehensil chisel-like teeth are on the premaxilla and dentary, while the crushing teeth are arranged in regular rows on vomerine and prearticular bones (Tintori, 1981; Nursall, 1996). The deep and flattened body of these fishes allowed them to move in complex environment and they probably were rather sluggish swimmers, feeding on hard-shelled invertebrates, corals or encrusting organisms. The body shape of *Endennia licia* n. gen. n. sp., being quite fusiform, completely covered by thick ganoid scales and furnished with rather small fins, does not suggest a similar mode of life. Nevertheless, in spite of the heavy squamation, the seemingly loose articulation between the scales could have improved the mobility of this fish, making it able to pursue moving preys. It might be therefore hypothesized that the anterior teeth were used for seizing small swimming organisms such as crustaceans, which were subsequently crushed with the grinding teeth. Anyway, we do not exclude other possible food among the invertebrates provided with harder mineralized parts, as molluscs or echinoderms, common in the Zorzino Limestone. These latter constituted a source of food that was previously underexploited by Middle Triassic actinopterygians, because of the primitive pattern of their skull, whose mobility was limited by the cheek bones jointed to the maxilla. On the contrary, the new arrangement of the skull bones of the neopterygians, with the consequently improved kinesis and the develop of a more powerful muscular system, allowed them to achieve more successful trophic adaptations. *Endennia licia* n. gen. n. sp. was able to reach full durophagy like the more advanced neopterygians, even if in a different way: it was not able to protrude the ethmoidal region, but the projecting marginal teeth and the differentiated crushing ones probably allowed it to improve its feeding capability.

CONCLUSIONS

After their extraordinary radiation during Anisian and Ladinian, "subholosteans" were thought to be a negligible presence in Late Triassic faunas: their only Norian representative was considered, for a long time, *Peltopleurus humilis* from Seefeld (Kner, 1867).

As new localities and new specimens were found, it became clear that this group was more widespread

and diversified than once supposed: some Late Triassic "subholosteans" achieved also high specializations, both in dentition and body morphology, in spite of their anatomical constraints and just before their last decline to extinction (Tintori & Sassi, 1992; Tintori & Lombardo, 1996).

One of these specialized forms is *Thoracopterus*, known from the Upper Triassic of Europe (Bronn, 1858; Bassani, 1895; Griffith, 1977; Tintori & Sassi, 1992). The representatives of this genus achieved the capability of gliding owing to the very long pectoral and pelvic fins (relate to standard length), associated to a hypobatic caudal fin (Tintori & Sassi, 1992). This kind of specialization, achieved independently, is found in extant Exocoetidae, teleostean "flying fishes" widespread in most temperate and tropical seas (Bertin, 1958; Bruun, 1935; Hubbs, 1932). The adaptation to glide achieved by the representatives of the family Thoracopteridae could have been used to feed upon other fishes, escape from predators, or may be related to long distance migrations (Tintori & Sassi, 1992). Probably in order to lighten the body weight, Norian *Thoracopterus* lacks the scale covering, but the trend to become lighter is clear also in other "subholostean" taxa. A new genus found in the early Norian of Lumezzane Member of Garza Valley (Brescia Prealps; Brunetti et al., 2001), currently under study, is in fact characterized by the absence of scales, except few dorsal and ventral rows between median and caudal fins; moreover, it shows the same anal fin modification, related to sexual dimorphism, seen in other peltopleuriforms and perleidiforms (Bürgin 1990, 1992; Lombardo 1999).

Differently from most of other perleidiforms, generally small and moderately fusiform fishes covered with heavy ganoid scales, *Gabanellia agilis*, from the Norian of the Zorzino Limestone, is characterized by a slender body, about 25 cm long, a very thin scale covering and a large, externally symmetrical and falcate tail. These features, in association with a powerful dentition made of conical, radially striated, uneven teeth, clearly indicate that *Gabanellia agilis* was a predator, good swimmer, probably able to keep high speeds for long distance, chasing small fishes in open waters (Tintori & Lombardo, 1996). It is worthy to note that neither in the Zorzino Limestone fauna, nor in other Triassic ones, there are large pelagic actinopterygians; among this group, the first large swimmers specialized for chase in open seas are the Jurassic *Caturus*, *Hypsocormus* and *Pachycormus*, all neopterygians fishes (Webb, 1984).

Among peltopleuriforms, new taxa have been recently found both in the Zorzino Limestone (CL, pers. obs.) and the Lumezzane Member; moreover, in the fauna of Garza Valley, a single specimen temporarily referred to the genus *Nannolepis* (Griffith, 1977) was found.

Therefore, the finding of *Endennia* n. gen., with its adaptation to strict durophagy, confirms once more both the considerable presence of "subholosteans" during the Norian and their extraordinary versatility, which allowed them to compete with the more advanced neopterygians.

ACKNOWLEDGEMENTS

The authors wish to thank G. Danini (Induno Olona) for the loan of specimen CM1SNIO 267 and S. Renesto for the photographs. The field-works in Zogno-Endenna sites, supported by a 40% grants from Ministero Istruzione Università e Ricerca, with the contribution of Bergamo Museum of Natural History "E. Caffi", were directed by A. Tintori, whose suggestions also greatly improved this paper. Earlier version of manuscript was improved by R. Mutter and C. Sorbini.

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Manuscript received 05 July 2004

Revised manuscript accepted 03 February 2005